

## Selection and Reproductive Success in Males of the Dragonfly, *Orthetrum japonicum* (Odonata: Libellulidae)

Eiiti KASUYA<sup>1)</sup>, Kaori EDANAMI and Ikuko OHNO

Laboratory of Biology, Faculty of Education, Niigata University, 2-8050 Ikarasi,  
Niigata City, 950-21 Japan

---

**Abstract.** Reproductive success, copulation success, and mating success were measured for a population of male dragonflies, *Orthetrum japonicum*. Copulation success explained the greatest variation in reproductive success. The proportion of copulations followed by oviposition was positively correlated with the number of oviposited eggs per mating. Directional selection on four morphological characters was estimated. The effect of selection on correlated traits was comparable to that of direct selection. Directional selection varied between traits and between episodes in a single trait. The probability that the observed directional selection on the four morphological traits was expected under the condition of the selective neutrality of traits was not smaller than 5%.

**Key words:** dragonfly, *Orthetrum japonicum*, reproductive success, selection.

---

### Introduction

In odonates (dragonflies and damselflies), lifetime reproductive success in natural populations has been measured in several species (McVey 1988; Fincke 1986; Koenig and Albano 1987; Anholt 1991). In particular, Koenig and Albano (1987) measured the directional selection on hind wing length, body mass, date on pond and time in flight. Anholt (1991) also measured the selection on morphological traits. Measuring both lifetime reproductive success and selection is essential in studies on selection during reproductive behavior. Reproductive success itself does not show selection but rather sets the upper limit of directional selection (Lande and Arnold 1983). The relationship between male odonate body size and his mating success has not been thoroughly examined (Higashi et al. 1987). However, male body size difference during territorial behavior has received increasing attention (Miller 1983; Fincke 1984b; Tsubaki and Ono 1987; Kasuya et al. 1987). Measuring the selection on morphological traits can present essential information on studies of sexual and natural selection. The development of the methods for analyzing selection made it possible to

divide observed selection into direct selection and indirect selection via other traits (Lande and Arnold 1983). In the present study, we measure the lifetime reproductive success in males of the dragonfly *Orthetrum japonicum* (Uhler) (Odonata: Libellulidae) and analyze selection on the morphological traits.

### Materials and methods

#### *Study area and observation*

Reproductive behavior of the dragonfly, *O. japonicum* was monitored at an abandoned field in Touzima, Maki, Niigata Prefecture, Japan, from the end of April to the beginning of June 1986. The dragonflies' reproductive behavior occurred in a temporally explosive manner, most reproductive activities were observed from May 13 to May 22, 1986. The observations were made from 8:00 to 16:00 each day. The study area included small pools and streams. The study area was about 650 m<sup>2</sup> and two observers were able to observe mating, ovipositing and territorial behavior in the entire area.

Males defended small territories over the water surface where they copulated with receptive females which flew to these territorial sites for oviposition. Males usually guarded ovipositing females after copulation (non-contact

---

<sup>1)</sup> To whom correspondence should be addressed.  
Present address: Department of Biology, Faculty of Science, Kyushu University,  
812-81 Fukuoka, Japan; E-mail: ekasuscb@mbox.nc.kyushu-u.ac.jp

post-copulatory guarding). The whole sequence of copulation and oviposition was usually observed in the territorial sites where the males copulated with females. Adult dragonflies were marked individually with a combination of paint dots on wings. Mark-recapture censuses showed that the migration of males between the study area and the neighboring pools was negligible. Males were observed during more than 95% of observations at the study area or the neighboring pools.

### *Characters measured*

Four morphological characters were measured: body width (the largest width of thorax), abdomen length (from the proximal base of the first abdominal segment to the apex of the abdominal appendage), wing length (from the apex to the hind wing base) and the head-thorax length (the length of head and thorax). Morphological measures were taken with a slide caliper to the nearest 0.1 mm (e.g. 1 mm = 10 units) and were log-transformed before analyses. Unless otherwise stated, transformed figures are reported.

### *Episodes of selection and fitness components*

We measured the number of copulations, the number of copulations which resulted in oviposition (the number of matings, hereafter), and the number of beatings of female abdomen on the water surface (the number of beatings, hereafter), for each individual male. The product of the number of beatings and the number of eggs oviposited per beating gives the fertility per mate. The number of eggs oviposited per beating was estimated to be  $25.6 \pm 6.6$  (mean  $\pm$  SD) by counting the number of beatings and the number of eggs oviposited in water filled in plastic vessels. Thus, the total number of beatings for an individual male multiplied by the constant (the number of eggs oviposited per beating, 25.6 in this case) gives an estimate of his lifetime reproductive success. However, we used the number of beatings instead of the estimated number of eggs in the present study, because multiplying by the constant (the number of eggs oviposited per beating) made no change in the values of relative fitness. In the present study, we measured the lifetime reproductive success on "unit" of beating. We call lifetime reproductive success simply reproductive success because we did not use "daily" measures of reproductive success in the present study.

We divided the number of beatings for an individual male (reproductive success) into three parts in a multiplicative form,  $W_1$  (the number of copulations; copulation success),  $W_2$  (proportion of the number of copulations resulting in oviposition to that of copulations) and  $W_3$  (the number of beatings per oviposition); thus

$W_1W_2$  is the number of matings of a individual male (mating success) and  $W_1W_2W_3$  is the total number of beatings for an individual male.

We followed Lande and Arnold (1983) and Arnold and Wade (1984a, b) for terminology and symbolism of analysis of selection if not otherwise mentioned. The symbols used are,  $W$ : absolute fitness,  $w$ : relative fitness (mean = 1),  $s$ : selection differential,  $\beta$ : selection gradient,  $i$ : selection intensity (selection differential standardized by SD of the trait),  $I$ : opportunity for selection,  $P$ : phenotypic variance-covariance matrix. The subscripts denote the episode of selection unless otherwise mentioned.

Out of 37 males of the population, 12 males copulated 74 times and 25 males did not copulate. In the 74 copulations, 49 resulted in oviposition while 25 copulations did not result in oviposition. We directly measured the number of beatings in 44 of 49 matings. In 4 matings, we estimated the number of beatings from the regression equation between the duration of oviposition and the number of beatings ( $y = 1.040x$ ,  $x$ : the duration of oviposition in s, and  $y$ : the number of beatings,  $n = 41$ ,  $r = 0.92$ ,  $P < 0.001$ ). In the remaining one mating, however, we were not able to measure the duration of oviposition or the number of beatings. We estimated the number of beatings in this one mating by the mean number of beatings of other matings of the male in question (the mean number of beatings per mating of this male was 137).

### *Assumptions and limitations of the data*

The first limitation of the data in the present study is that some oviposition did not occur immediately after copulation. Such ovipositions without copulation were observed when there were no or only a small number of territorial males especially during sudden cloudiness. The relative contribution of the ovipositions without copulation to the total number of fertilized eggs is estimated as 24.6% on the basis of the number of beatings (1,812 beatings in oviposition without copulation, and 5,563 in oviposition following copulation). We did not include them in the analyses in the present study. This is equivalent to assuming that the sire of eggs by oviposition without copulation is proportional to that by oviposition following copulation.

Second, we assumed complete 'last male priority' in sperm competition, i.e. a male which copulated with the female immediately prior to oviposition is assumed to be the sire of all the eggs oviposited by a female per oviposition bout. This seems a reasonable assumption because a specialized organ on the 'penis' for removal of sperm of a preceding male was described in this genus (Siva-Jothy 1984), and because of the results of studies on sperm competition in other odonates (Waage 1979, 1983; McVey and Smittle 1984; Fincke 1984a, Siva-Jothy and Tsubaki

1994; see also Koenig and Albano 1987).

Third, we assumed that the number of eggs oviposited per beating of female abdomen on the water surface was constant. In reality, egg number might be dependent on temperature or other factors and might not be constant (Fincke 1985).

There were 37 males in the population studied. This small population was not a subsample of a large population, but represented an adult population where immigration and emigration were negligible.

### *Statistical tests of the selection differentials and gradients*

Selection differentials and gradients for traits can occur by chance even when the traits are selectively neutral. The evaluation of the hypothesis that the observed selection is due to randomness alone may be important since the population size in the present study was small (37 males). Regression analyses, under the conditions of normality and homogeneity of variances, can evaluate the probability that the observed or stronger selection is expected under the selective neutrality. However, these conditions are questionable for the fitness components and traits in the present study. We also made randomization tests free from these restrictions.

Several methods of randomization are possible in the present case. We needed to quantify the probability that the observed or stronger selection (differential or gradient) is obtained when the trait is selectively neutral. We made randomizations where individuals with the observed traits were randomly assigned to an observed fitness. We randomly assigned trait vectors (consisting of the four traits) of individuals to the fitness components. We defined the selection parameters to be stronger than the observed one when the absolute value of the parameter was larger than the observed one. We used three fitness components,  $W_1$ ,  $W_1W_2$  and  $W_1W_2W_3$ . We made 10,000 permutations of random assignments (Edgington 1995).

We analyzed the effect of variation in copulation success on selection parameters by randomization tests. Some selection can be detected by the stochastic effect even when the trait in question is selectively neutral. Stronger selection parameters can be observed under selective neutrality when the variation in the copulation success is larger. The variation in copulation success, 4.83 ( $I$ , Table 1), was much larger than that under the random copulation scenario ( $I=0.5$ ). We examined the effect of variation in copulation success by randomization. We assumed that a female copulated with males at random with the same probability (reciprocal of the number of males). In this randomization scheme, the distribution of the copulation success of males is binomial (see Sutherland 1985). By comparing the results of this randomization and Table

**Table 1.** Opportunities for selection.

Source of variance in relative fitness	Contribution to total selection		
	Symbol	Value	% <sup>1</sup>
Copulation success	$I_1$	4.83	94.8
	$I_2$	0.06	1.1
Cointensities (1st and 2nd episodes)	*	0.31	6.1
No. of beatings per oviposition	$I_3$	0.20	4.0
Cointensities (1st, 2nd and 3rd episodes)	*	-0.30	-5.9
Total selection	$I$	5.10	100

$I_2$ : proportion of number of copulations to that of copulations which resulted in oviposition.

\*: cointensities include all the covariance terms between current episode and all the prior episodes, as in Koenig and Albano (1987).

<sup>1</sup>: the sum of terms is not equal to total because of rounding.

3, we can evaluate the effect of variation in copulation success on selection parameters under selective neutrality. We use this procedure only for copulation success because it makes biological sense only in this case.

## Results

### *Reproductive success and opportunity for selection*

Table 1 shows the opportunities for selection (the variance of relative fitness) in each episode. Mean  $\pm$  SD of absolute fitness was  $2.00 \pm 4.40$  ( $W_1$ ),  $1.32 \pm 3.02$  ( $W_1W_2$ ),  $150.35 \pm 339.54$  ( $W_1W_2W_3$ ), respectively. The first episode (copulation success) explains the greatest part of the total opportunity for selection. The cointensity terms contributed only 0.2%. However, two cointensity terms canceled out each other (6.1% and -5.9%). Because cointensity terms of the opportunity for selection are not readily interpretable, we used the correlation from the test of the relationship between fitness components. There was a significant positive correlation between  $W_2$  and  $W_3$  ( $r=0.659$ ,  $P<0.05$ ,  $n=12$ ). Other correlations were not significant ( $r=-0.290$ ,  $P>0.2$  for  $W_1$  and  $W_3$ , and  $r=-0.180$ ,  $P>0.5$  for  $W_1$  and  $W_2$ ,  $n=12$  for both cases).

In several studies of lifetime reproductive success and selection of odonates, reproductive span or days alive was considered as a selective episode (Fincke 1986; Koenig and Albano 1987). As mentioned in Materials and Methods, we did not measure the reproductive span of males.

For comparison, the correlations between the territorial duration and the four morphological traits were made. They were 0.197 for body width, 0.132 for abdomen length, 0.068 for wing length, and -0.093 for head-thorax

length, respectively. All correlations were not significant ( $P > 0.5$  for the four traits). The correlation between the copulation efficiency (copulation success divided by territorial duration) and the four morphological traits was not significant ( $r = 0.436$  for body width,  $r = -0.360$  for abdomen length,  $r = -0.433$  for wing length, and  $r = -0.056$  for head-thorax length, respectively,  $n = 10$  and  $P > 0.1$  for all the cases).

Although the opportunity for selection gives important information, this parameter only sets the upper limit of the selection ( $|i| < I^{1/2}$ ) and is not a measure of selection on a given trait (Lande and Arnold 1983).

### Directional selection on four morphological traits

Values of mean  $\pm$  SD in mm (coefficient of variation in parenthesis) of the four morphological traits before selection before log-transformation were  $6.1 \pm 0.4$  (6.2%) for body width,  $29.5 \pm 1.1$  (3.7%) for abdomen length,  $32.9 \pm 1.5$  (4.6%) for wing length and  $15.2 \pm 1.2$  (7.8%) for head-thorax length. Correlations among the four traits were 0.438 between body width and abdomen length, 0.318 between body width and wing length,  $-0.022$  between body width and head-thorax length, 0.313 between abdomen length and wing length,  $-0.119$  between abdomen length and head-thorax length, 0.174 between wing length and head-thorax length, respectively ( $n = 37$ ). Correlations between head-thorax length and the other three traits were not significant while those among the other three traits were significantly positive at the 5% level.

The selection differential ( $s$ ), selection gradient ( $\beta$ ) and selection intensity ( $i$ ) are shown in Table 2. The selection differential represents both the direct selection on the trait and selection on correlated traits while the selection gradient represents only the direct selection on the trait. The selection differentials and the selection gradients are not on the same scale. Therefore, it is not easy to evaluate the contribution of the direct selection force on the trait in question and the indirect effect due to selection on correlated traits from the values of the selection gradients and differential. We use the relationship,  $s_i = \sum P_{ij} \beta_j$  (Lande and Arnold 1983) (subscript denotes the trait in this case; e.g.  $s_i$  is the selection differential of the  $i$ -th trait, and  $P_{ij}$  is the phenotypic covariance of the  $i$ -th and  $j$ -th traits), to divide the selection differential into the direct selection component ( $P_{ii} \beta_i$ ) and indirect ones (other terms). Table 2 shows the relative contribution of selection on each trait based on this relationship. This shows that the selection on correlated characters was not negligible in several cases. In particular, in abdomen length of the first episode and body width of the second episode, the sign of the contribution of direct selection on the trait itself is opposite to that of the selection differential (observed selection). The directional selection on each of the four mor-

**Table 2.** Selection differentials and selection gradients of the four morphological traits.

#### (a) body width

Episode	$s$ (direct, indirect)	$i$	$\beta$	mean
1	0.028 (0.033, -0.005)	0.460	8.563	4.104
2	-0.003 (0.001, -0.004)	-0.053	0.175	4.132
3	-0.007 (-0.003, -0.004)	-0.112	-0.679	4.129
Total	0.018 (0.031, -0.013)	0.296	8.059	4.122

#### (b) abdomen length

Episode	$s$ (direct, indirect)	$i$	$\beta$	mean
1	0.004 (-0.007, 0.011)	0.010	-5.187	5.685
2	-0.004 (-0.004, 0.000)	-0.011	-2.698	5.689
3	-0.005 (-0.002, -0.003)	-0.012	-1.116	5.684
Total	-0.005 (-0.012, 0.007)	-0.013	-9.000	5.680

#### (c) wing length

Episode	$s$ (direct, indirect)	$i$	$\beta$	mean
1	0.002 (0.001, 0.001)	0.050	0.408	5.795
2	-0.004 (-0.003, -0.001)	-0.095	-1.355	5.797
3	-0.007 (-0.007, 0.000)	-0.156	-3.270	5.793
Total	-0.009 (-0.009, 0.000)	-0.201	-4.216	5.785

#### (d) head-thorax length

Episode	$s$ (direct, indirect)	$i$	$\beta$	mean
1	-0.034 (-0.036, 0.002)	-0.427	-5.474	5.021
2	-0.002 (-0.002, 0.000)	-0.024	-0.304	4.987
3	0.009 (0.011, -0.002)	0.114	1.673	4.985
Total	-0.027 (-0.027, 0.000)	-0.336	-4.104	4.994

$s$ : selection differential,  $i$ : selection intensity (selection differential divided by the standard deviation of the trait before selection),  $\beta$ : selection gradient, and mean: mean of trait before selection (in "Total", mean after selection is shown).

phological traits was not similar to each other. Selection differentials of the four traits had the same sign only in the second episode. Further, none of the selection gradients of these traits had the same sign in any of the episodes (Table 2).

The directional selection on each of the four morphological traits changed between episodes. None of the selection differentials of any of the four traits had the same sign between episodes. For all the traits, the selection differentials of the first and third episodes had opposite signs. Only the selection gradient of abdomen length had the same sign in all the episodes. Though the opportunity for selection in the first episode explains most of the total

**Table 3.** Partial regression coefficients in multiple regression of absolute fitness against the four morphological traits.

fitness component	$W_1$	$W_1 W_2$	$W_1 W_2 W_3$
body width	17.60 (0.207, 0.197)	11.89 (0.215, 0.206)	1245.42 (0.252, 0.234)
abdomen length	-10.66 (0.647, 0.643)	-10.73 (0.504, 0.497)	-1390.84 (0.446, 0.435)
wing length	0.84 (0.962, 0.961)	-1.29 (0.916, 0.914)	-651.61 (0.637, 0.626)
head-thorax length	-11.25 (0.245, 0.221)	-7.86 (0.238, 0.213)	-634.17 (0.399, 0.370)
$R^2$	0.090	0.089	0.071

numbers in parenthesis: (significant probability by  $t$ -test, significant probability by randomization)

opportunity for selection (Table 1), directional selection in the first episode explains most of the total selection only in body width and head-thorax length.

We tested the significance of selection by a multiple regression of fitness components against values of traits and by randomization tests. Regression assumes a normal distribution and homogeneity of variances. Table 3 shows the result of tests by both procedures. The number of significant probabilities found in the randomization tests was constantly smaller than that found in the conventional multiple regression. All selection differentials and gradients were not significantly different from zero at the 5% level.

Table 4 shows the results of randomization under the random copulation regime. The observed (or stronger than observed) selection differentials and gradients are expected with smaller probabilities than in the observed variation in copulation success (Table 3). Several significant probabilities (body width and head-thorax length) were smaller than 5%. The comparison of Tables 3 and 4 shows that the variation in copulation success affects how strong selection parameters are observed under selective neutrality.

## Discussion

### *Opportunities for selection*

Fincke (1986) and Koenig and Albano (1987) used the episodic division of opportunity for selection in males of odonates. Because our episodes are different from theirs, we can make comparisons only of mating success and reproductive success. The comparison of our results and those of *Plathemis lydia* (Drury) by Koenig and Albano (1987) is of special interest because both exhibit resource defense polygyny (Koenig and Albano 1987). The value of  $I$  (opportunity for selection) for reproductive success

**Table 4.** Probability of obtaining selection parameters stronger than observed under the condition of random copulation (result of 10,000 random permutations).

(a) selection differential

	trait			
	body width	abdomen length	wing length	head-thorax length
probability	0.000	0.198	0.338	0.001

(b) selection gradient

	trait			
	body width	abdomen length	wing length	head-thorax length
probability	0.000	0.077	0.449	0.001

in the present study (5.10) is much larger than those in *Enallagma hageni* (Walsh) (1.402) and *P. lydia* (2.99). This difference is due to the difference in  $I$  for mating success. This is 5.20 in our study, 1.040 in *E. hageni* and 2.73 in *P. lydia*. The major contribution of  $I$  of mating success to that of reproductive success is common for these studies (74% in *E. hageni* and 91% in *P. lydia* and 102% in ours). The contribution of eggs/mating to the opportunity for total selection is relatively small in all the three studies.

The reproductive period of a population was quite short in *O. japonicum*, only 10 days (net 8 days), much shorter than *E. hageni* and *P. lydia*. This suggests that the difference in survivorship of males does not have a major effect in *O. japonicum* contrary to the odonates with longer reproductive periods (Fincke 1986; Koenig and Albano 1987). Territorial duration explains the most variation in mating success (73.3%) in *O. japonicum*. However, territorial duration is not indicative of survivorship of males in *O. japonicum* because a considerable number of non-territorial males were observed. This suggests that the contribution of the difference in survivorship is small in *O. japonicum* and that factors other than male survivorship could have an important effect on male mating success.

The positive correlation between  $W_2$  and  $W_3$  means that a male with a higher ratio of mating success to copulation success, made females oviposit more eggs per mating. This suggests a functional relationship between the ability to maintain a territory against other males and that of guarding ovipositing females. Or this could suggest a correlation between two different scenes of female choice.

The variation in the reproductive success ( $W_1 W_2 W_3$ ) in the present study was large. Reeve and Keller (1995) and others have estimated the degree of concentration of

reproductive success to certain member(s) of a population by using the indices of 'reproductive skew'. An index of reproductive skew (Reeve and Keller 1995) is given by  $(N_b v + N_n)/(N_b + N_n)$ , where  $N_b$  is the number of breeding members in a population,  $N_n$  is that of non-breeding ones and  $v$  is the variance among breeding members in reproductive success divided by the maximum possible value of the variance, respectively. The values of the index of reproductive skew in *O. japonicum* were 0.703 based on  $W_1 W_2 W_3$ , 0.704 based on  $W_1 W_2$  and 0.701 based on  $W_1$ , respectively. These values are comparable to those in some primitively eusocial insects and social vertebrates (Reeve and Keller 1995).

### Patterns of directional selection

In Koenig and Albano (1987) and this study, the only common character analyzed is hind wing length (here, simply referred as wing length). In both *P. lydia* and *O. japonicum*, the total selection differential and gradient of wing length was negative. However, the selection differential and gradient in oviposition per mating (our third episode) was positive in *P. lydia* but negative in *O. japonicum*. In both species, selection intensities on wing length were on the order of  $10^{-1}$  or  $10^{-2}$  SD. In *O. japonicum*, wing length of males was weakly negatively correlated with the number of beatings by females when males engaged in complete guarding (Kasuya et al. personal observation). The difference of directional selection in oviposition per mating between *P. lydia* and *O. japonicum* suggests a different role for wings during this episode between two species.

In the present study, the selection differentials and gradients varied with the morphological trait and with the episode of the same morphological trait. This suggests that the conclusions of the studies on the strength and direction of selection based on a single body size measurement are suspect. This could justify the criticism made by Arnold and Wade (1984b) on 'the single trait myopia'.

We did not find a positive correlation between the value of opportunity for selection and the absolute value of selection differential in an episode in any of the four traits. Also, the difference in directional selection among the traits was very large. These show that the patterns of directional selection is hard to estimate from the opportunities for selection. As shown in Arnold and Wade (1984a, b), opportunities for selection only show the upper limit of directional selection.

We failed to find statistically significant selection pressure on the four morphological traits. The analysis of directional selection, however, suggested possible types of several functional significance for the morphological traits in reproductive behavior. The selection during the first episode favored larger body width, and the effects of selec-

tion on the correlated traits were small (14.9% of the selection differential) in this case. The selection differential in this episode was much larger than that in the other two episodes. Body width of territorial residents was significantly larger than that of intruders in territorial conflicts (Kasuya et al. 1997). This suggests that the analysis of episodic selection is a useful tool for identifying possible candidates that have a functional significance for reproductive behavior. Though proving the functional relationship is not the purpose of the selection episode analysis.

Selection during the third episode favored the shorter abdomen length. Probably this was due to the negative correlation between abdomen length and the number of beatings by females when males engaged in complete guarding (Kasuya et al. personal observation). The white abdomen color of sexually active males in *O. japonicum* suggests it has a signal function to females. This negative correlation suggests that the number of eggs sired by a male is determined by females as the effect of male-male competition is probably weak when males engaged in complete guarding. Female choice during oviposition might be responsible for selection on a morphological trait of males in this case. In the analysis of selection, both complete and incomplete guarding were included.

### Probability of observing strong selection under neutrality

Randomization used to examine the statistical significance of selection parameters (Table 3) does not assume the normal distribution and homogeneity of variances that may be violated in the analysis of selection. The randomization results (Table 3) gives the probability that the observed or stronger level of selection can be obtained under selective neutrality of the trait. No trait in our study had a probability smaller than 5% in directional selection. However we believe that the importance of the probability results should extend beyond simple significance testing below a certain level (e.g. 5%).

The comparison of the probabilities generated by randomizations in Tables 3 and 4 illustrates the effect of the large opportunity for selection. The value of  $I$  ( $I_1$ : 4.83, Table 1) is about ten times as large as that of  $I$  in the case of random copulation (Table 4). The larger the value of opportunity for selection, the more likely the large value of selection parameters will be observed under the selective neutrality.

**Acknowledgments:** We are indebted to O. Fincke and W. D. Koenig for critical reading of early versions of the manuscript. Thanks are also due to T. Nishida, Y. Tanaka and Y. Tsubaki for discussions. A part of this study, analysis of data in particular, was supported by a Grant-in-Aid (No. 07640838) from the Ministry of Education, Science and Culture.

## References

- Anholt, B. R. (1991) Measuring selection on a population of damselflies with a manipulated phenotype. *Evolution* **45**: 1091–1106.
- Arnold, S. J. and M. J. Wade (1984a) On the measurement of natural and sexual selection: theory. *Evolution* **38**: 709–719.
- Arnold, S. J. and M. J. Wade (1984b) On the measurement of natural and sexual selection: applications. *Evolution* **38**: 720–734.
- Edgington, E. S. (1995) *Randomization tests*, 3rd edn. Marcel Dekker, New York.
- Fincke, O. (1984a) Sperm competition in the damselfly, *Enallagma hageni* (Odonata: Coenagrionidae): benefits of multiple mating to males and females. *Behavioral Ecology and Sociobiology* **14**: 235–240.
- Fincke, O. (1984b) Giant damselflies in a tropical forest: reproductive biology of *Megaloprepus coerulatus* with notes on *Mecistogaster* (Odonata: Pseudostigmatidae). *Advances in Odonatology* **2**: 13–27.
- Fincke, O. (1985) Alternative mate-finding tactics in a non-territorial damselfly (Odonata: Coenagrionidae). *Animal Behaviour* **33**: 1124–1137.
- Fincke, O. (1986) Lifetime reproductive success and the opportunity for selection in a nonterritorial damselfly (Odonata: Coenagrionidae). *Evolution* **40**: 791–803.
- Higashi, K., K. Ubukata and Y. Tsubaki (1987) *Dragonfly mating systems*. Tokai Univ. Press, Tokyo. (in Japanese)
- Kasuya, E., Y. Mashima and J. Hirokawa (1987) Reproductive behavior of the dragonfly, *Orthetrum japonicum*. *Journal of Ethology* **5**: 105–113.
- Kasuya, E., K. Edanami and I. Ohno (1997) Territorial conflicts in males of the dragonfly, *Orthetrum japonicum* (Odonata: Libellulidae): The role of body size. *Zoological Science* **14**: 505–509.
- Koenig, W. D. and S. S. Albano (1987) Lifetime reproductive success, selection and the opportunity for selection in the white-tailed skimmer *Plathemis lydia*. *Evolution* **41**: 22–36.
- Lande, R. and S. J. Arnold (1983) The measurement of selection on the correlated characters. *Evolution* **37**: 1210–1226.
- McVey, M. E. (1988) The opportunity for sexual selection in the dragonfly *Erythemis simplicicollis*. pp. 44–58. In T. H. Clutton-Brock (ed.) *Reproductive success*. Univ. Chicago Press.
- McVey, M. E. and B. J. Smittle (1984) Sperm precedence in the dragonfly *Erythemis simplicicollis*. *Journal of Insect Physiology* **30**: 619–628.
- Miller, P. L. (1983) The duration of copulation correlates with other aspects of mating behavior in *Orthetrum chrysostigma* (Burmeister) (Anisoptera: Libellulidae). *Odonatologica* **12**: 227–238.
- Reeve, H. K. and L. Keller (1995) Partitioning of reproductive success in mother-daughter versus sibling associations: a test of optimal skew theory. *American Naturalist* **145**: 119–132.
- Siva-Jothy, M. T. (1984) Sperm competition in the family Libellulidae with special reference to *Crocothemis erythraea* and *Orthetrum cancellatum*. *Advances in Odonatology* **2**: 195–207.
- Siva-Jothy, M. T. and Y. Tsubaki (1994) Sperm competition and sperm precedence in the dragonfly *Nannophya pygmaea*. *Physiological Entomology* **19**: 363–366.
- Sutherland, W. J. (1985) Chance can produce a sex difference in variance in mating success and explain Bateman's data. *Animal Behaviour* **33**: 1349–1352.
- Tsubaki, Y. and T. Ono (1987) Effect of age and body size on the male territorial system of the dragonfly, *Nannophya pygmaea* Rambur. *Animal Behaviour* **35**: 518–525.
- Waage, J. (1979) Dual function of the damselfly penis: Sperm removal and transfer. *Science* **203**: 916–918.
- Waage, J. (1983) Sperm competition and the evolution of odonate mating systems. pp. 251–290. In R. L. Smith (ed.) *Sperm competition and the evolution of animal mating systems*. Academic Press, New York.

Received 20 February 1997; Accepted 27 October 1997